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Life-History Variation Among Three Temperate Hermit Crabs: The Importance of Size in Reproductive Strategies

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Abstract. The supply and quality of empty gastropod shells may play important roles in the ecology and evolution of hermit crabs. We compare the life histories of three subtidal hermit crabs in Nantucket Harbor, Massachusetts: *Pagurus annulipes, P. longicarpus,* and *P. pollicaris.* Specifically, we examine seasonal patterns of reproduction in females, male and female size structure, reproductive effort, and temporal patterns of larval abundance. We also compare shell size among the three species. Life-history features vary with size among the three species. The smallest species (*P. annulipes*) reproduce soon after metamorphosis and have a high reproductive effort. The two larger species (*P. longicarpus* and *P. pollicaris*) delayed reproduction to an intermediate size, and have lower reproductive efforts than *P. annulipes.* There is no effect of body size on reproduction in *P. annulipes,* but there is a strong positive effect in *P. longicarpus* and *P. pollicaris.* Seasonal patterns of early stage larvae correlated with seasonal patterns of ovigery in all three species, with highest larval densities sampled in *P. annulipes* and *P. longicarpus.* Size differences among species were related to patterns of shell usage. Male and female *P. annulipes* were always found in large shells relative to body size. In comparison, male and female *P. longicarpus* and *P. pollicaris* were found in small shells compared to body size. We suggest that early maturity and high reproductive effort have evolved in response to a high risk of mortality associated with small shells. Delayed maturity and low reproductive effort are favored in species that reach a size refuge from shell-crushing predators. Effects of shell limitation are more likely to be common in large species and may also be an important selective in shaping hermit crab life histories.

Introduction

Studies on the ecology and evolution of hermit crabs (Decapoda, Anomura) have often focused on the consequences of limited shell resources. Hermit crabs are dependent on an external shelter to protect them from physical stress and predation (Reese, 1969). Typically, empty gastropod shells are used as mobile shelters, but a few species may also live within sponges and other animals. Because hermit crabs cannot manufacture their own shells, they are entirely dependent on the processes that make suitable shells available for their use, including snail mortality and intra- and inter-specific shell exchanges (Hazlett, 1981). Three observations are commonly used to support the hypothesis that shells are in short supply: (1) empty shells are often rare in habitats that support hermit crab populations (Hazlett, 1970; Childress, 1972; Kellogg, 1976; Abrams, 1978, 1980; Bertness, 1980), (2) natural populations of hermit crabs are often in smaller shells than preferred in laboratory experiments (Vance, 1972; Bach *et al.*, 1976; Abrams, 1978; Scully, 1979; Bertness, 1980), and (3) hermit crabs often have ritualized shell-exchange behavior (reviewed by Hazlett, 1981) that may be beneficial when shell resources are scarce.

Field experiments have shown effects of limited shell supply at the population and community level. Vance (1972) added shells to an experimental reef on the coast of Washington State during a one-year period, increasing the density of *Pagurus hirsutiusculus* compared to a control reef where no shells were added. In the tropics, Bach *et al.* (1976) and Bertness (1981a) found that competitive subordinates occupied smaller shells when competitive

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dominants were present, compared to when competitive dominants were absent. In the Bay of Panama (Bertness, 1981a), experimental addition of shells to tide pools containing three potential competitors increased rates of shell acquisition by competitive dominant species compared to subordinate species. Thus, interactions within species and among co-existing species may both be affected by shell supply.

Variation in the supply and quality of shell resources may affect hermit crab life histories. In the tropics, Bertness (1981b) found clutch size and size at maturity to respond to shell supply. Experimental treatments in which shells were added increased the size at maturity and reduced clutch size in several tropical species. In this example, a phenotypically plastic reproductive strategy was hypothesized as a way in which hermit crabs could maximize fitness when confronted with changing resource levels. Shell quality and supply may also vary with shell size. For example, small shells are generally less effective deterrents to shell-crushing predators than larger shells (Bertness and Cunningham, 1981; Borjesson and Szelistowski, 1989; Buckley and Ebersole, 1994). In addition, small shells are typically more abundant than large shells (Hazlett, 1981; D. B. Carlon, pers. obs.). The negative effects of shell limitation may therefore be more common in hermit crabs that use large shells compared to small shells. These size-specific selective pressures associated with shell resources may have important consequences for hermit crab life histories.

In this paper, we compare and contrast size distributions, effects of size on reproduction, individual reproductive allocation, and seasonal patterns of reproductive activity among three *Pagurus* hermit crabs in a temperate New England harbor. We then show how shell size varies among species. We suggest that hermit crab life histories have evolved in response to size-specific mortality patterns. Early maturity and high reproductive effort are favored when the risk of adult mortality is high. In contrast, delayed reproduction and low reproductive effort are optimal when the risk of adult mortality is low and shells are rare.

Materials and Methods

Study location and species

Nantucket Harbor is a temperate, semi-enclosed coastal lagoon located on Nantucket Island, Massachusetts. The shallow harbor (max. depth <10 m) has a sandy bottom with deeper areas covered with the shell remnants of gastropods (especially *Crepidula* spp.) and bay scallops (*Aequipecten irradians*). Eelgrass (*Zostera marina*) forms dense stands in shallow regions (<3 m). Surface temperature may range from 0°C in the winter to 25.5°C in late summer, and complete freeze-over occurs in some, but not all, winters (W. Tiffney, pers. obs.).

Three hermit crab species commonly occur in Nantucket Harbor: *Pagurus annulipes* (Stimpson), *Pagurus longicarpus* (Say), and *Pagurus pollicaris* (Say). *P. longicarpus* occurs in both littoral and subtidal zones, often near or within patches of eelgrass. *P. annulipes* is only found subtidally, typically at depths >4 m. This species appears to prefer coarse sediments that occur in tidal channels within the harbor. The third species, *P. pollicaris,* is found in littoral and subtidal habitats. The shell species most commonly used vary among the three species. *P. annulipes* is almost always found in two *Anachis* spp.: *A. avara* and *A. translirata.* In comparison, *P. longicarpus* uses several species, most commonly: *Littorina littorea, Nassarius trivittatus,* and *Polinices duplicatus. P. pollicaris* is also found in several species: *Lunatia heros, Polinices duplicatus,* and *Busycon canaliculatum.*

Adult features

To determine male and female size distributions and temporal patterns of reproductive activity, benthic populations were sampled weekly from March to October of 1990. This period was chosen because previous work in Nantucket Harbor and the Cape Cod region indicated that the reproductive season for these three *Pagurus* species begins in early spring and ends in late summer (Nyblade, 1970; Johnson and Ebersole, 1989, unpub. data). Hermit crabs were sampled at two sites separated by 3 km within the harbor. The first site, First Bend, is in a tidal channel near the harbor entrance. The second site, Quaise, is located on the eastern shore of the harbor, close to the University of Massachusetts Field Station. In March and April, crabs were sampled by boat-towed scallop dredge. Though scallop dredges employed in Nantucket Harbor have a large mesh size (2.5 cm), hermits as small as 2.0 mm carapace length were captured due to clogging of the net with shells, eelgrass, and macroalgae. From May through October, crabs were sampled by divers using scuba, and a sample consisted of every crab found during a 45-min dive. There were no significant differences between the sizes of crabs collected by these two different methods. In the laboratory, each crab was removed from its shell by drilling a small hole in the shell apex with an electric drill and then tickling the abdomen with a thin piece of monofilament line. Hermit size was determined by measuring the distance from the rostrum to the edge of the calcified portion of the carapace with vernier calipers [equivalent to the whole carapace measurement of Markham (1968)]. Sex was determined by the position of the gonopores and pleopod morphology (McLaughlin, 1980). Female reproductive condition was scored as ovigerous if an extruded egg mass was attached to the pleopods. To determine temporal patterns in female reproductive activity (proportion of the sample ovigerous), weekly samples were pooled for each month. At least two benthic samples were taken per month, and typically four were taken from April to September. One sample was collected during the last week of March and the first week of October.

The relationship between female size and reproduction was determined by constructing species-specific size categories (Table I). Size categories were chosen so that similar numbers of individuals were distributed among three categories. The association between size and reproduction was tested for each species with a two-way contingency table defined by size (three categories) and reproductive condition (ovigerous or non-ovigerous). The log-likelihood statistic (G^2) was used for all tests of significance. Tests of significance were robust to the choice of size classes for size comparisons.

To compare reproductive allocation among the three species, females were collected during August 1990 and May 1991. Estimates of reproductive allocation in *P. pollicaris* sampled in August 1990 could not be determined because no ovigerous females were sampled on this date. Female *P. pollicaris* were collected near the First Bend site and female *P. annulipes* and *P. longicarpus* were collected at the Quaise site. Each crab was removed from its shell and fixed in a 5% formalin-seawater solution. Eggs of all individuals were in a similar developmental condition: the eggs were a rich purple and no differentiation was visible. Eggs were carefully removed from the pleopods with forceps and placed in a preweighed petri dish. Eggs and somatic tissue were weighed to the nearest 0.001 g after drying at 100°C for 48 h. Pilot studies showed that water content stabilizes after two days. Reproductive allocation was estimated as the dry weight of eggs divided by the dry weight of somatic tissue. A two-way analysis of variance (ANOVA) was used to compare reproductive allocation between species and sampling dates. In this analysis there were two levels of the factor "species": *P. annulipes* and *P. longicarpus;* and two levels of the factor "date": August 1990 and May 1991. Both factors were considered fixed in the analysis. A single factor ANOVA was used to compare reproductive allocation among the three species during May of 1991. Individual means were compared with the Tukey HSD method. Reproductive allocation data remained heteroscedastic [determined by Cochran's test (Winer *et al.*, 1991)] after a number of transformations. Following the recommendations of Underwood (1981) and Winer *et al.* (1991), untransformed data were used in both ANOVAs, and significance tests were interpreted conservatively. All statistical tests were performed with Systat software (Systat, Inc., Evanston, IL).

Table I

Size of three hermit crab species (carapace length) in three size categories used in the analysis of the relationship between body size and reproduction

	Size category (mm)		
Species	Small	Medium	Large
Pagurus annulipes	1.9–3.1	3.2–3.5	3.6–4.6
P. longicarpus	2.2–5.0	5.1–7.0	7.1–12.0
P. pollicaris	5.4–14.6	14.7–22.0	22.1–34.7

Temporal patterns of larval availability

To determine the seasonal pattern of larval abundance, plankton tows were made weekly from March to October 1991. On each date, two surface tows were made at five stations located at 1.5-km intervals along the principal axis of the harbor (SW–NE). All tows were taken between 1000 hours and noon. Volume of water sampled was determined with a mechanical flow-meter (General Oceanics #2030). After collection, each sample was halved with a plankton splitter and preserved in 5% buffered formalin. In the laboratory, samples were sorted with a dissecting microscope to species and stage of development using the keys of Nyblade (1970), Roberts (1970), and Sadler (1984). Mean abundances were calculated on each date by pooling the two replicate samples from five sites (n = 10). There was no difference among species in patterns of spatial abundance within the harbor: larval abundances were high at stations near the harbor entrance and decreased with distance from the entrance. Because very few megalops stage larvae were sampled (n = 3), they were combined with stage zoea 4 larvae for analysis.

Patterns of shell size among species

To determine if shell size relative to crab size varied among species, each crab collected during 1990 was assigned to a shell size/crab size category. Categories were determined by tapping the claws of a crab to encourage retraction, viewing the aperture, and noting how far the claws and walking legs extended beyond the aperture. Four categories were defined: Category 1 = no part of crab visible; Category 2 = tips of claws visible; Category 3 = first segment of major claw visible; Category 4 = second segment of major claw visible. The four categories ranged from a high shell size/crab size ratio (Category 1 = large shell, small crab) to a low shell size/crab size ratio (Category 4 = small shell, large crab). Heterogeneity of shell fit among species was tested with a two-way contingency table defined by three levels of species (*P. annulipes, P. longicarpus,* and *P. pollicaris*) and the four shell-fit categories. Independence among species was tested with the log-likelihood statistic.

Results

Reproductive features

Female *P. longicarpus* (mean carapace length = 5.9 mm) were almost twice as large as *P. annulipes* (mean carapace length = 3.3 mm) and much smaller than *P. pollicaris* (mean carapace length = 19.1 mm) (Fig. 1). Mean size of females correlated with size at maturity: the smallest *P. annulipes* found with eggs was 2.2 mm, whereas the smallest ovigerous *P. longicarpus* was 3.8 mm. The species with the largest females, *P. pollicaris*, matured at the largest size; the smallest ovigerous female was 13.4 mm carapace length. Males of *P. annulipes* and *P. longicarpus* were significantly larger than conspecific females (Student's t-test for paired comparisons, $t = -6.945$, df = 380, $P < 0.001$; and $t = -4.008$, df = 1012, $P < 0.001$, respectively), but there was no difference in size between sexes in *P. pollicaris* (Fig. 1; $t = 0.341$, df = 171, $P = 0.734$).

The probability of reproduction does not increase with size in the smallest species, *P. annulipes*, but does increase with size in the two larger species: *P. longicarpus* and *P. pollicaris* (Fig. 2). In *P. annulipes* there was no difference in the percentage of ovigerous females in the small, medium, and large size categories ($G^2 = 5.29$, df = 2, $P = 0.071$). When all three categories are combined, 68.9% of the *P. annulipes* females were ovigerous during 1990. In contrast, there was a strong effect of size on the probability of reproduction in *P. longicarpus* ($G^2 = 32.72$, df = 2, $P < 0.001$) and *P. pollicaris* ($G^2 = 13.15$, df = 2, $P = 0.001$); the probability of reproduction increased with increasing size in both species. The proportion of ovigerous *P. longicarpus* and *P. pollicaris* was less than *P. annulipes* during 1990, with 33% of female *P. longicarpus* ovigerous and 36.9% of female *P. pollicaris* ovigerous.

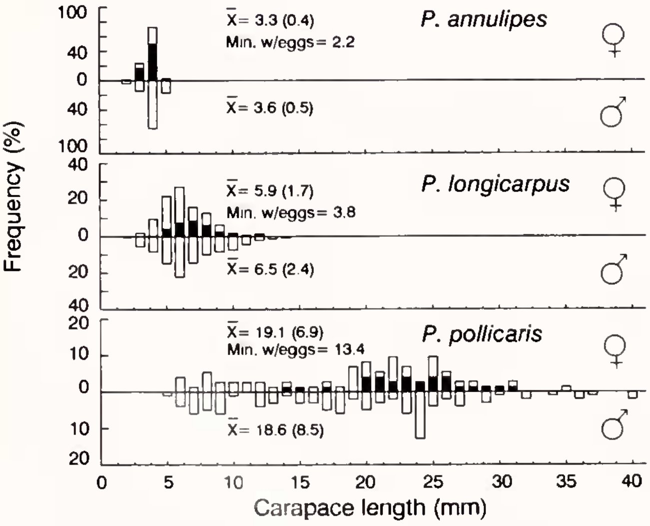

Figure 1. Size distribution of three *Pagurus* hermit crabs. Dark bars are ovigerous females. Standard deviations are given in parentheses. Total sample sizes are 382 for *P. annulipes*, 1022 for *P. longicarpus*, and 174 for *P. pollicaris*.

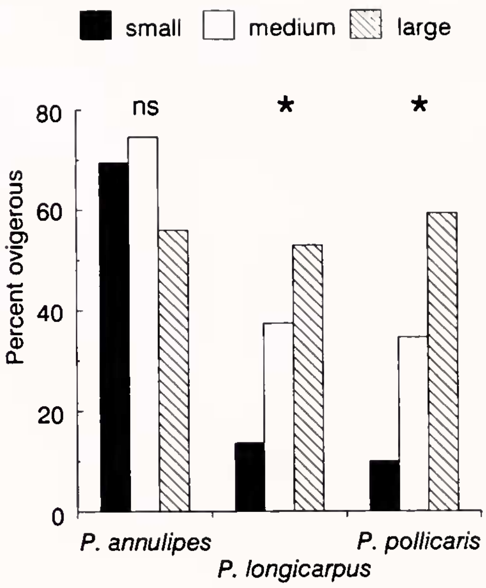

Figure 2. The distribution of ovigerous females in three size categories for three hermit crab species. Stars indicate a statistically significant effect of size on probability of ovigery at the 0.05 level of significance. See Table I for definition of the size categories for each species. Sample sizes = 238 for *P. annulipes*, 303 for *P. longicarpus*, and 73 for *P. pollicaris*.

Reproductive allocation was highest in the smallest species, *P. annulipes*, and lower in the two larger species, *P. longicarpus* and *P. pollicaris* (Fig. 3). In August 1990 *P. annulipes* females allocated 49.5% dry body weight to reproduction. The following spring (May 1991) allocation in *P. annulipes* decreased to 32.6% but was still greater than *P. longicarpus* on either sampling date or that of *P. pollicaris* (sampled only in May 1991). The reproductive allocation of *P. longicarpus* was similar on the two sampling dates: 25.1% in August 1990 and 25.8% in May 1991. *P. pollicaris* sampled in the spring of 1991 had the lowest allocation of any of the three species at 20% dry body weight. Considering the reproductive allocation of *P. longicarpus* and *P. annulipes* on the two sampling dates, a two-way ANOVA indicated a significant interaction between species and date ($F_{1,109} = 8.07$, $P < 0.005$, Table II), confirming the decline in *P. annulipes* reproductive allocation from the late summer 1990 to the spring 1991. The effect of species remained highly significant ($F_{1,109} = 25.02$, $P < 0.001$) in this analysis, much more so than the effect of date ($F_{1,109} = 6.78$, $P = 0.01$). Considering the effect of species on reproductive allocation during 1991,

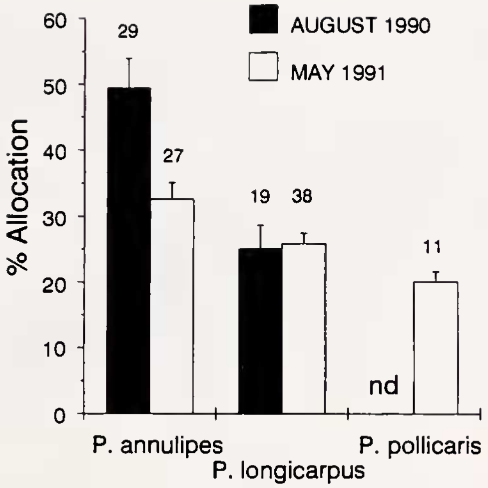

Figure 3. Reproductive allocation among three hermit crabs on two dates. Reproductive allocation = total dry weight of brood/(total dry crab weight–dry weight of brood). Vertical bars are standard errors and sample sizes are given above error bars. See text for statistical interpretation. No data (nd) were collected for *P. pollicaris* during August 1990 due to a lack of reproductive activity at this time.

a one-way ANOVA revealed a significant effect of species ($F_{2,73} = 6.20$, $P = 0.003$), and *post hoc* comparison of the means using the Tukey HSD procedure revealed a significant difference between *P. annulipes* and both *P. longicarpus* ($P = 0.039$) and *P. pollicaris* ($P = 0.004$) but no significant difference between *P. longicarpus* and *P. pollicaris* ($P = 0.205$).

There were striking differences in seasonal patterns of reproductive activity among the three species (Fig. 4). A single ovigerous *P. annulipes* was collected on 28 April; however, both males and females were extremely scarce at this time. By 15 May, individual *P. annulipes* had emerged from the sediments and were easily collected. The proportion of ovigerous females increased from 38% in May to 82% in June and remained high (>60%) until September, when a mean of 39.8% of the population was ovigerous. The reproductive season appeared to be over by 6 October, when 29 females were collected and none was ovigerous. In contrast to *P. annulipes*, active *P. longicarpus* and *P. pollicaris* were collected at the earliest sampling date of 31 March. No ovigerous specimens of *P. longicarpus* were observed on this date ($n = 3$), but reproductive activity was high during the following month of April, with a mean of 85.7% ovigerous. Reproduction declined during May and June to 0% in July but increased to 19.3% in August and 8.3% in September. None of 15 *P. longicarpus* females collected on 6 October was ovigerous. Five of the eight female *P. pollicaris* collected on 31 March were ovigerous. Reproductive activity was high in April with a mean of 81.3% ovigerous, and declined during May and June to 0% during the months of July, August, and September. No *P. pollicaris* females were collected on the last sampling date of 6 October. From these data, it is apparent that *P. annulipes* has high reproductive activity from late spring through the summer; *P. longicarpus* reproduces mainly in the spring, with a second smaller peak in August; *P. pollicaris* has the shortest reproductive period, with all reproduction occurring in the spring.

All three species are capable of producing multiple broods. Unfertilized eggs were often observed in the abdominal ovaries of ovigerous females in all three species, particularly as the extruded, fertilized eggs approached the last stage of development (eye spots clearly visible through egg cuticle).

Temporal patterns of larval availability

Temporal patterns in the availability of first stage larvae (zoea 1) generally reflected temporal patterns of reproductive activity in the three species (Figs. 4, 5). *P. annulipes* larvae were sampled in highest density on 14 June (2.06 larvae m^{-3}) and were collected in low densities (0.012–0.536 larvae m^{-3}) from June to September (Fig. 5a). *P. longicarpus* zoea 1 larvae were found earlier in the season compared to *P. annulipes* larvae: a mean density of 6.16 larvae m^{-3} was sampled on 18 May. *P. longicarpus* zoea 1 larvae occurred at low densities (<1 larvae m^{-3}) from June to September (Fig. 5b). The first zoeal stage of *P. pollicaris* was sampled at greatest densities on 29 May and 30 June, with mean densities of 0.16 and 0.075 larvae m^{-3} collected respectively (Fig. 5c). While availability of zoea 1 larvae generally reflected temporal patterns of reproductive activity of benthic adults, there were two dates when larvae were found in the water column but adult reproductive activity was not detected in Nantucket Harbor. No ovigerous *P. longicarpus* were sampled during the month of July (Fig. 4), yet low densities of zoea 1 larvae (<0.334 larvae m^{-3}) were collected on three dates during this month. Similarly, *P. pollicaris* zoea 1 larvae were sampled in low abundance (<0.034 larvae m^{-3}) at three times during September, even when no reproductive activity in adults was detected after June (Fig. 4). These

Table II

*ANOVA table evaluating effects of two dates (August 1990 and May 1991) and two species (*Pagurus longicarpus *and* Pagurus pollicaris*) on reproductive allocation*

Source	df	MS	*F*	*P*
Date	1	0.175	6.783	0.010
Species	1	0.644	25.024	<0.001
Date × Species	1	0.208	8.067	0.005
Error	109	0.026		

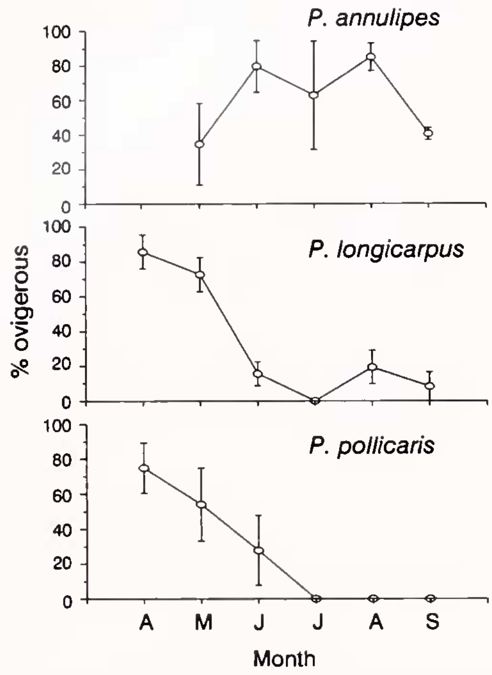

Figure 4. The percentage of ovigerous females collected in benthic samples for three *Pagurus* hermit crabs during the spring, summer, and fall of 1990. Means and standard errors (vertical bars) were calculated from samples collected weekly during each month. Single samples collected in April for *P. annulipes* and in October for all three species are not included because a mean could not be calculated.

results are most likely due to an influx of larvae produced at other locations, where the timing of adult reproduction may differ from Nantucket Harbor (Williams, 1984).

Fewer larvae were found for *P. pollicaris* than for *P. annulipes* and *P. longicarpus*. This was especially apparent in the later larval stages (no zoea 4 and megalops *P. pollicaris* larvae were found in 1990 harbor samples). Abundances of later stage larvae (zoea 2, 3, 4, and megalops) were comparable for *P. annulipes* and *P. longicarpus*. The maximum mean density of *P. annulipes* and *P. longicarpus* zoea 3 sampled was the same at 0.209 larvae m^{-3} (Fig. 5a, b). Larval availability was also similar for the last larval stages (zoea 4 and megalops). In these two species, two peaks in mean density of larvae (>0.01 m^{-3}) were recorded during the summer months (Fig. 5a, b).

Patterns of shell size among species

P. annulipes inhabited larger shells compared to body size than either *P. longicarpus* or *P. pollicaris* (Fig. 6). Greater than 80% of *P. annulipes* were found in shell size/crab size category 1 and <3% were found in categories 3 and 4. By comparison, *P. longicarpus* and *P. pollicaris* were more likely to have lower shell size/crab size ratios. Only 45.2% of *P. longicarpus* and 53.8% of *P. pollicaris* were found in category 1, and the percentages of these two species in shell fit categories 2, 3, and 4 were much higher than for *P. annulipes*. A two-way contingency table defined by hermit crab species and shell size/crab size category indicated that the distribution of individuals in the four categories varied among species (G^2 = 192.53, df = 6, $P < 0.001$). Comparisons of shell size/crab size categories between species indicated that there was no difference in the distribution of categories between *P. longicarpus* and *P. pollicaris* (G^2 = 6.96, df = 3, P = 0.073). However, the distribution of categories was significantly different between both *P. annulipes* and *P. longicarpus* (G^2 = 188.75, df = 3, $P < 0.001$) and between *P. annulipes* and *P. pollicaris* (G^2 = 63.42, df = 3, $P < 0.001$).

Discussion

Seasonal reproductive effort is evidently higher in smaller hermit crab species. The reproductive strategy of *P. annulipes*, the smallest species, includes the traits of early maturity after metamorphosis, high reproductive allocation per brood, and high reproductive activity throughout the spring and summer. In contrast, *P. pollicaris*, the largest species, uses a very different strategy, delaying reproduction until achieving large body size, allocating a low proportion of energy per brood, and becoming reproductively active only in the spring. The reproductive strategy of *P. longicarpus* appears to lie somewhere between *P. annulipes* and *P. pollicaris*. Reproductive effort per brood is lower than in *P. annulipes* but not statistically different from that of *P. pollicaris*. On the other hand, *P. longicarpus* females reach maturity at relatively small body size, are reproductive over a longer period than *P. pollicaris*, and are reproductively active in the spring and summer months, like *P. annulipes*.

The relationship between size and life-history traits described here was also found in the hermit crab fauna of the Pacific coast of Washington State. Nyblade (1974) compared reproductive traits among 16 intertidal and subtidal hermit crab species that spanned a broad size range. His data show a strong positive relationship between average body size and minimum size at ovigery (R^2 = 0.511, $F_{1,14}$ = 14.622, P = 0.002; data from table 4.10). There is also a negative relationship between body size and annual reproductive effort (larval production female body weight^{-1} year^{-1}; R^2 = 0.325, $F_{1,14}$ = 7.918, P = 0.021; data from tables 4.7a and 4.10). In Nyblade's study, small intertidal species typically matured at a small body size and had large annual reproductive efforts. In comparison, large subtidal species delayed reproduction and had low annual reproductive efforts. The relationship between size and life history traits seen in *Pagurus* hermit crabs of Nantucket Harbor may be a general phenomenon among other hermit crab assemblages.

An explanation for the reproductive strategies documented here and elsewhere lies in the risk of mortality associated with using different sized shells. Small shells are more easily damaged or destroyed by shell-crushing predators than are larger shells (Bertness and Cunningham, 1981; Borjesson and Szelistowski, 1989; Buckley and Ebersole, 1994). It follows that the risk of mortality should be greater for species or size classes inhabiting small shells compared to large shells. Hermit crabs that use small shells as adults (*e.g., P. annulipes*) will have high adult mortality due to their susceptibility to shell-crushing predators. The juveniles of large species will also have high mortality rates; however, adults can potentially escape in size by using shells that are immune to shell-crushing predators (*e.g., P. longicarpus* and *P. pollicaris*). Several life-history models predict early maturity and high reproductive effort when adult mortality is high, and delayed maturity and low reproductive effort when juvenile mortality is greater than adult mortality (Gadgil and Bossert, 1970; Schaffer, 1974; Law, 1979; Michod, 1979; Charlesworth, 1980). Age-specific mortality is therefore a potential selective mechanism that explains the life-history variation observed in the hermit crabs of Nantucket Harbor as well as on the coast of Washington.

As Reznick and Endler (1982) have pointed out, size-specific predation can mediate intraspecific competition. When predators eat small juveniles, the larger adults tend to accumulate in populations. Increased intraspecific competition among adults is predicted to select for delayed maturity and a decrease in reproductive investment (MacArthur and Wilson, 1967). Large hermit crab species may experience the negative effects of intraspecific competition more commonly than smaller species due to their immunity to shell-crushing predators, and the general scarcity of suitable shells. The high shell size/crab size ratios observed in the small *P. annulipes* and the low shell size/crab size ratios in the larger *P. longicarpus* and *P. pollicaris* are consistent with the hypothesis that the effects of intraspecific competition (*e.g.,* reduced shell availability) are more common in large species. However, this interpretation of shell size/crab size ratios assumes that all three *Pagurus* species prefer large to small shells. Because no selection experiments were conducted in Nantucket Harbor, variation in shell size preference among species can also explain the observed pattern. Nevertheless, increased intraspecific competition among adults is predicted in populations where adult mortality is low. If size-selective predation is important in hermit crabs in general, then selective pressures associated with intraspecific competition may also contribute to life-history variation.

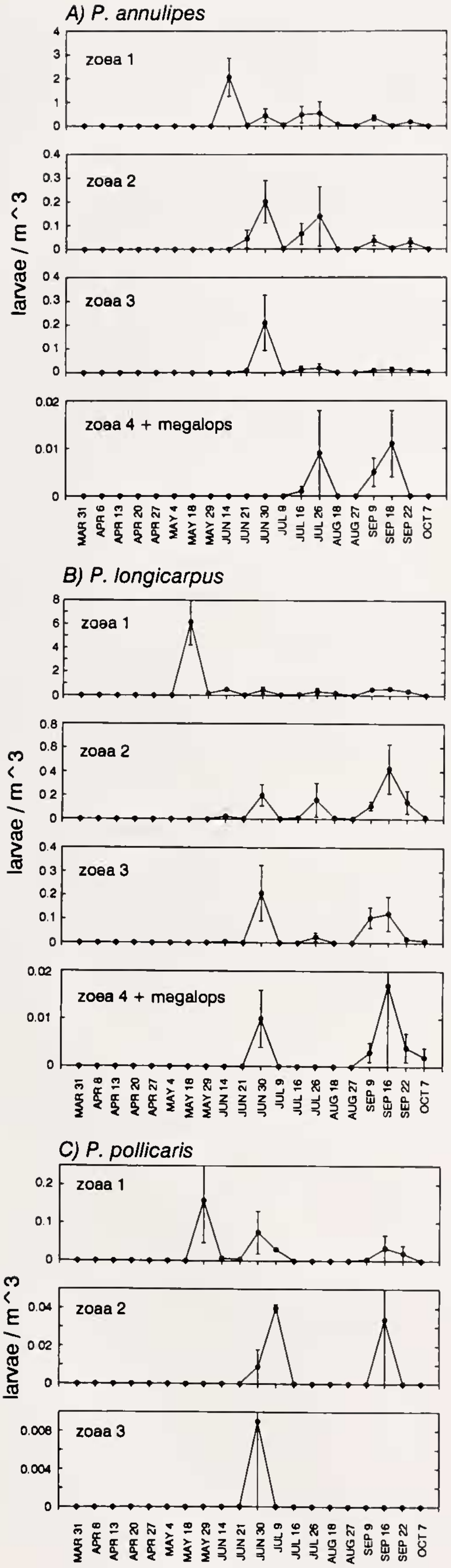

Figure 5. Temporal abundance of four stages of larvae from three hermit crab species (A, B, and C) during 1990. Means and standard errors (vertical bars) calculated from 10 plankton tows on each date. No zoea 4 or megalops larvae were collected for *Pagurus pollicaris* during 1990.

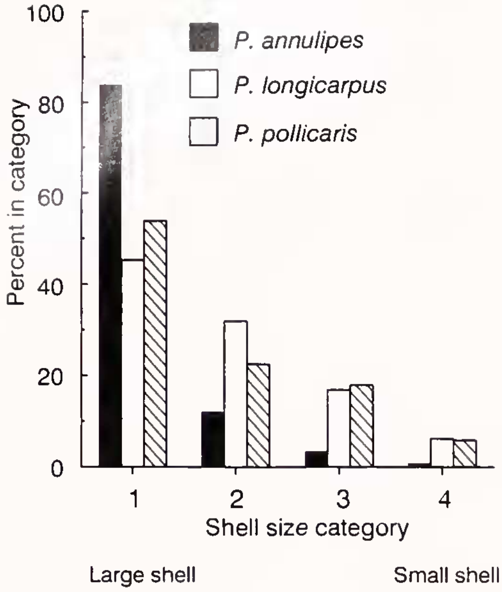

Figure 6. The distribution of three hermit crab species in four categories of shell size. See text for definition of shell size categories. Sample size for each species is the same as in Figure 2.

Reproductive allocation in *P. annulipes* was >15% higher in August 1990 than in May 1991. One explanation for this pattern is that female size varied between samples. However, this was not the case: there was no significant difference in female size between samples (*t*-test for paired comparisons, $t = -0.373$, df = 54, $P = 0.711$). A more likely explanation for this pattern is related to strong seasonal changes in water temperature in Nantucket Harbor. Water temperature in Nantucket Harbor may vary by as much as 10°C between May and August (Carlon, 1991). If growth and reproduction are temperature-dependent in *P. annulipes*, then colder spring temperatures may result in reduced reproductive allocation compared to the late summer when water temperature reaches its maximum.

Within a species, the importance of body size on reproductive decisions varied among the three species. It appears that body size does not play an important role in reproductive decisions of *P. annulipes*, with reproduction by females of every size. In comparison, there was a strong positive effect of body size on reproduction in the two larger species (*P. longicarpus* and *P. pollicaris*). This pattern supports the idea that *P. annulipes* has a high reproductive effort throughout its lifetime: females reach maturity quickly and reproduce regardless of body size. Size plays a more important role in the reproductive decisions of *P. longicarpus* and *P. pollicaris*. Two mechanisms may explain this pattern. The first is that maturity is typically delayed until a large body size is reached. This would increase the likelihood of sampling large ovigerous females. The second mechanism involves inter-sexual mate selection. Active choice of larger females over smaller females by males would result in higher fertilization rates of large females. Interestingly, Harvey (1991) found that male *Clibanarius digueti* does not select a female mate on the basis of body size in the Gulf of California. He also found no relationship between body size and the probability of being ovigerous in this species. *Clibanarius digueti* is similar in size (males 4.69 mm, females 3.38 mm) to *P. annulipes* in this study. Thus, it is possible that strong sexual selection for female body size is unimportant in small species but may play a more important role in larger species such as *P. longicarpus* and *P. pollicaris*.

Patterns of larval abundance in Nantucket Harbor were consistent with the higher seasonal reproductive efforts of *P. annulipes* and *P. longicarpus*. Early stage larvae of *P. annulipes* were 20 times more abundant and larvae of *P. longicarpus* 80 times more abundant than *P. pollicaris* larvae at the peak of reproduction. These differences are even more apparent in the later stages, with only a single zoea 3 larva of *P. pollicaris* sampled during 1990, and no zoea 4 or megalops sampled at all. Previous sampling of Nantucket Harbor gave the same result (Carlon, 1991): only two zoea 3 larvae and one zoea 4 larva of *P. pollicaris* were collected during 1989 with a similar sampling effort. The ranking of larval abundances among species was the same in 1989 and 1991 (*P. longicarpus* > *P. annulipes* ⋙ *P. pollicaris*). On the Washington Coast, Nyblade (1974) measured hermit crab recruitment rates with settlement traps and found that species with high seasonal larval outputs also had high recruitment. The large number of larvae produced by *P. longicarpus* and *P. annulipes* throughout the summer may increase the probability of successful settlement and metamorphosis compared to *P. pollicaris*.

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